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Climate effects on demographic parameters in an unhunted population of Alpine chamois (*Rupicapra rupicapra*)

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Because of a rapidly changing climate, the need to understand how populations respond to varying climatic conditions has become increasingly important. Using long-term data from an unhunted population of Alpine chamois (*Rupicapra rupicapra*) and autoregressive time series models we investigated the extent to which the population demography was affected by local climate. Because density and weather are likely to operate differently on various sex–age categories, anticipated effects were assumed to vary among categories. Generally, elevated densities in 1 year negatively influenced the subsequent change in population size. Severe snow conditions during late winter negatively affected total population growth, and growth of the male, yearling, and juvenile segments of the population. A lagged effect of early winter snow on the change in animal numbers was demonstrated for females. Winter temperatures positively affected the growth rate of juveniles, whereas they appeared to have negative consequences for male and yearling growth rates. The juvenile–female ratio was negatively affected by the current female density, but did not respond to the various climate variables. Winter survival of juveniles was negatively influenced by the juvenile number during the preceding summer and harsh snow conditions during early winter. Our results indicate that winter climate shapes the demography of Alpine chamois. Particularly, winters with a lot of snow might have long-lasting consequences for the population. Considering the juveniles, lagged effects apparently operate through the body condition of their mothers. The conflicting effects of temperature on the different sex–age categories make the direction of expected population response to global warming difficult to predict.

Key words: Alpine chamois, autoregressive time series model, climate change, population dynamics, rain, snow, temperatures, ungulate, weather

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During the past decades, awareness has risen that the rapidly changing climate has severe consequences for whole ecosystems (Walther et al. 2002). Therefore, one major concern of ecologists is to evaluate the potential responses of plant and animal populations to varying climatic conditions (Visser 2010). Recent studies suggest that organisms that inhabit extreme environments year-round could be strongly affected by these changes (e.g., Jenouvrier et al. 2009; Ozgul et al. 2010; Parmesan 2006).

Mountain ungulates represent 1 group for which investigating climate effects on population dynamics is appealing because they inhabit alpine or arctic environments and have to cope with harsh and highly variable environmental conditions. Although changes in the growth of ungulate populations might to some extent be due to variation in climatic conditions during periods of vegetation growth (Loison et al. 1999; Pettorelli et al. 2007), winter conditions appear to be one of the major extrinsic factors driving these

populations (Grotan et al. 2008; Jacobson et al. 2004; Mysterud and Ostbye 2006; Solberg et al. 2001).

Climate likely affects the various age–sex classes of ungulate populations differently (Coulson et al. 2001). Young and senescent animals have lower energy reserves and higher metabolic needs (Hudson and White 1985). Therefore, they are generally considered to be more sensitive to adverse climatic conditions as well as to high densities than prime-aged animals (Solberg et al. 2001). Similarly, adult males of polygynous species have elevated reproductive costs during the mating season compared with adult females (Bobek et al. 1990; McElligott et al. 2003; Mysterud et al. 2004, 2008), which makes them particularly vulnerable to situations that require the use of stored body reserves to endure unfavorable climatic conditions and periods of food shortage. Because of their differential ability to respond to challenging environments, the varying sensitivity of different sex–age classes has to be taken into account when analyzing extrinsic and intrinsic effects on sex and age-structured ungulate populations.

In the present study, we analyzed demographic processes in a population of Alpine chamois (*Rupicapra rupicapra*) on the basis of a complete time series of 19 years. Alpine chamois are polygynous mountain ungulates exhibiting moderate sexual dimorphism in body size (Garel et al. 2009). Depending on the ecological conditions, females can reach sexual maturity at about 1.5 years of age (Baur 1985; Pioz et al. 2008a), whereas males seem to participate actively in rutting activities from the age of 2.5 years onward (Krämer 1969). Mating normally takes place in early winter, particularly during November and December (Willisch and Ingold 2007). During that time of the year, adult males incur high energetic costs while simultaneously exhibiting a strong rut-related hypophagia (Willisch and Ingold 2007). Together these effects likely contribute to dramatic losses in body weight (Schröder 1971) and consequently in fat reserves of males during the rut. The parturition period in Alpine chamois typically spans from mid-May to mid-June, and females normally give birth to a single juvenile per year.

The aim of our study was to identify how climatic effects are operating on the different sex–age classes of this mountain ungulate population that inhabits an extreme alpine environment year-round. Therefore, we evaluated the changes in population growth for the various categories separately. Because recruitment of juveniles is known to be a major factor in the dynamics of ungulate populations (Post and Stenseth 1999; Solberg et al. 1999; Wang et al. 2002), we also investigated which climate variables influenced fecundity of females and survival of juveniles during winter. In agreement with previous studies on Alpine chamois (Jonas et al. 2008; but see Loison et al. 1999) and other mountain ungulates (Crampe et al. 2002; Gonzalez and Crampe 2001; Grotan et al. 2008; Jacobson et al. 2004), we expected snow conditions during the winter to be important for their demography. Considering that the body condition of animals is typically deteriorating over the course of the winter, we predicted that late winter conditions would be crucial for population growth. On the basis of our arguments presented above, we further predicted that young animals and males would be most affected by climatic variations, whereas adult females would show a weaker response (Gaillard et al. 1998, 2000). Last, in accordance with other studies (Coulson et al. 2000; Wang et al. 2002), we expected the fecundity of females to be positively affected by mild winter air temperatures.

Materials and Methods

Study area and animals.—The study area was located above the timber line in the Augstmatthorn National Game Reserve, northeast of the village Interlaken in the Swiss Alps (46°45′N, 7°56′E). It is characterized by a southwest-to-northeast-running mountain ridge with open alpine pastures spreading between 1,350 and 2,137 m, rocky cliffs, and scree slopes. Throughout the winter, the north side of the ridge is normally covered by snow, whereas the sun-exposed parts of the south side are often free of snow due to solar radiation and avalanches.

The study population was under close investigation in the years 1964–1966 (Krämer 1969) and 1989–2002 (e.g., Gander and Ingold 1997; Schnidrig-Petrig and Ingold 2001). The surveillance of marked and radiocollared animals during those periods indicated that the study area was inhabited year-round by males and at least 3 groups of females with their offspring. Animals typically occupied the open habitat above the timberline and only rarely retreated to the forests located at lower elevations. Outside of the mating season, adult males lived socially segregated from the females in loose aggregations with other males. Yearling females normally stayed within the nursery groups, whereas yearling males roamed the study area in small peer groups. Although the study population is not a closed system, adult Alpine chamois exhibit a high level of site fidelity (for the population—Krämer 1969; in general—Hamr 1985), and dispersal distances of young animals are known to be relatively short (Loison et al. 2008). Furthermore, there is no indication that immigration and emigration rates would differ between our study area and nearby areas. Consequently, we believe that migration and dispersal of animals do not markedly influence the abundance of chamois in our study area.

Population census data.—Animal censuses in the study area started in 1990. Each year, we performed multiple censuses on consecutive days during summer after the parturition period (i.e., late June and July) and during late autumn before the beginning of the winter (i.e., October and November). During the censuses, multiple observers ($\bar{X} = 7.8 \pm 1.5$ *SD*) simultaneously counted all animals that were present within their view. The observers were located on specific vantage points that permitted a virtually complete overview of the whole study area. Prior analyses showed that the detectability of animals around mid-day, when Alpine chamois typically exhibit a low activity (Boldt 2003; Ingold et al. 1998), is reduced (C. S. Willisch, pers. obs.). Therefore, we used only censuses that began either early in the morning or late in the afternoon. Single censuses lasted between 60 and 90 min. This sampling scheme resulted in 61 censuses

Table 1.—Definitions and brief descriptions of the various climate variables that have been considered in this study to explain population dynamics in Alpine chamois (*Rupicapra rupicapra*) in the Augstmatthorn National Game Reserve, Switzerland.

Climate variable	Definition	Brief description
SnowD_NDJ	Average daily snow depth of November, December, and January (cm)	Snow depth during early winter
SnowD_FMA	Average daily snow depth of February, March, and April (cm)	Snow depth during late winter
SnowF_NDJ	Cumulative daily snowfall of November, December, and January (cm)	Snowfall during early winter
SnowF_FMA	Cumulative daily snowfall of February, March, and April (cm)	Snowfall during late winter
Rain_JJA	Cumulative daily rainfall of June, July, and August (mm)	Summer rainfall
Temp_NDJ	Average daily air temperature of November, December, and January (°C)	Temperature during early winter
Temp_FMA	Average daily air temperature of February, March, and April (°C)	Temperature during late winter
Temp_JJA	Average daily air temperature of June, July, and August (°C)	Temperature during summer

between 1990 and 2008, with on average 3.2 ± 1.7 (mean ± *SD*) censuses per year.

We conducted observations using spotting scopes from distances of <1,500 m. Recorded animal categories were: juveniles (≤1 year of age), yearlings (1 to 2 years of age), adult males (≥2 years of age), and adult females (≥2 years of age). We determined the age and sex of animals on the basis of morphological traits (i.e., body size, size and shape of horns, presence and expression of primary and secondary sexual traits) and behavioral characteristics (e.g., posture while urinating, body contact with juveniles—Crampe et al. 2002; Schröder and von Elsner-Schack 1985). Animals that could not be assigned to one of the specified categories were recorded as "undetermined animals." On average this category accounted for 8.7% ± 7.0% ($\bar{X}$ ± *SD*) of all animals observed during single censuses.

Because we could not assign all animals to one of the specific age–sex classes listed above, we reassigned group members of aggregations containing undetermined animals (i.e., 579 of 5,025 total aggregations, or 11.5 %) to the various age–sex categories using an empirically derived distribution key. The key was based on all recorded aggregations of chamois that were fully determined ($n = 4{,}446$). We evaluated the compositions of these aggregations depending on the presence or absence of juveniles and yearlings, the sex of observed animals, as well as the size of the recorded aggregations (see Appendices I and II, online supplementary information). The derived proportions were then used to reassign group members of the concerned aggregations on a fractional base to the different sex–age categories. This reassignment procedure did not influence the total population counts, and was statistically conservative for all other measures because it was based on average values derived from the total data set collected over 19 years. Therefore, the detection of relationships between demographic parameters and climatic variables is unlikely to be artificially favored by the reassignments. For the subsequent analyses, we used the average numbers of animals that were observed in the different sex–age categories during the summer and autumn censuses to obtain consistent estimates for the different demographic parameters. Data collection was approved by the Swiss Federal Office of the Environment (FOEN), and conformed to guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

Climate variables.—We obtained information on the climatic conditions from 2 nearby weather stations (for snow: Hasliberg: 1,825 m; 46°45′N, 8°13′E; provided by the Swiss Federal Institute for Snow and Avalanche Research; for temperatures and precipitation: Interlaken: 580 m; 46°40′N, 7°52′E; provided by the Federal Office of Meteorology and Climatology MeteoSwiss) that have been shown to closely reflect the climatic conditions in the study area (C. S. Willisch, pers. obs.). The definitions of the various climate variables that were considered for our analyses are listed in Table 1. The variables summarize the prevailing weather conditions (snow, precipitation, temperatures) over a 3-month periods covering early (November to January) and late winter (February to April) when forage quality and availability are normally limited, and snow and low air temperatures are straining the energy budgets of animals; and mid-summer (June to August) when high-quality food typically is abundant and animals are restoring their fat reserves.

Statistical analyses.—Statistical computations were performed in R (version 2.12.2—R Development Core Team 2011). To evaluate the impact of the climate variables on demographic parameters, we fitted autoregressive models using the R package "dyn" (version 0.2–8—Grothendieck 2009). We accounted for effects of population density on the population growth rate by the inclusion of animal density in the year $t - 1$. Significant negative relationships were considered as evidence of negative density dependence (Solberg et al. 2001). To examine the effects of density dependence and climate (V) on growth in the different sex–age categories, we parameterized various Gompertz and Ricker models, which are 2 of the most commonly used models for density-dependent growth (Lele et al. 1998). For our analyses population change was defined as $y = \ln(n_t/n_{t-1})$; where n_t is the number of animals in the population at time t. Consequently the corresponding Gompertz models took the form:

$$y = a + b*\ln(n_{t-1}) + c*V_i + d*\varepsilon \quad (1)$$

and the Ricker models:

$$y = a + b*n_{t-1} + c*V_i + d*\varepsilon \quad (2)$$

where a, b, c, and d are the autoregressive coefficients and ε represents the stochastic contribution from noise and unmodeled processes.

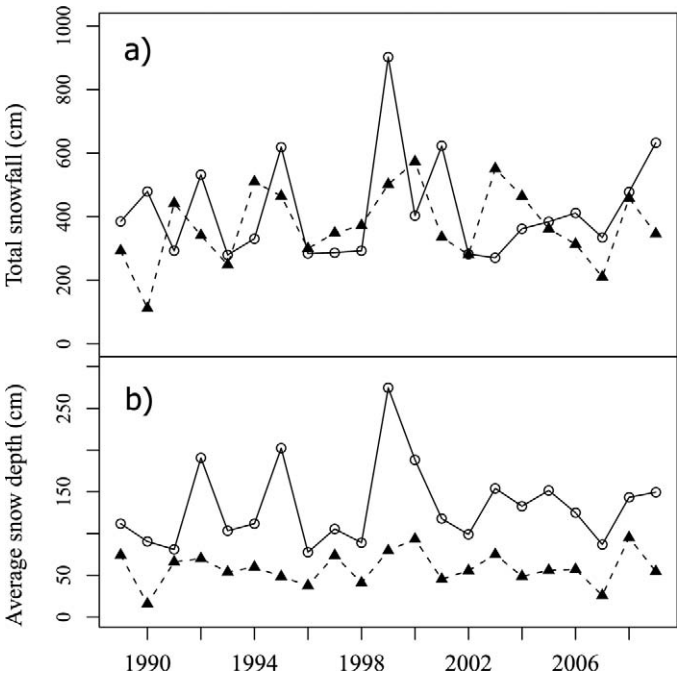

Fig. 1.—a) Interannual variation in the cumulative snowfall and b) the average snow depth for the period of November to January (filled triangles) and February to April (open circles) between 1989 and 2009, measured at the Hasliberg Weather Station, Switzerland (snow data provided by the Swiss Federal Institute for Snow and Avalanche Research, 2008).

To analyze the extent to which fecundity of females (measured as the number of juveniles per number of females at time t) and winter survival of juveniles (measured as the number of observed yearlings at time t per number of observed juveniles observed at time $t - 1$) were affected by animal densities and the various climate variables, we applied logistic regression models with binomial error distributions and logit link functions (Crawley 2007). In the corresponding models, the response variables (i.e., fecundity and juvenile survival) were implemented as vectors. The fecundity vector contained the number of juveniles and the number females at time t, whereas the vector for winter survival of juveniles contained the number of yearlings at time t and the number of juveniles at time $t - 1$.

We applied stepwise backward regression to evaluate the influence of the climate variables on the demographic parameters. The full model contained information on the climatic conditions (snow and temperatures) during the current winter at time t and the previous winter at time $t - 1$, as well as the preceding summer period at time $t - 1$. We used the Akaike information criterion corrected for small sample size (AIC_c) to choose the most parsimonious model (Hurvich and Tsai 1989).

Results

Seasonal weather conditions.—With regard to the snow conditions, the winters between 1989 and 2008 exhibited strong interannual variation (Fig. 1). Cumulative snowfall averaged around 374 ± 119 cm ($\bar{X} \pm SD$) for the November–January period (i.e., early winter period) and around 412 ± 159 cm for the February–April period (i.e., late winter period). Corresponding average snow depths were 58.6 ± 20.5 cm and 131.9 ± 50.1 cm for the 2 periods, respectively. Extreme values were recorded for the late winter in 1999, when the cumulative snowfall exceeded 900 cm and the average snow depth measured 274 cm. Mean daily air temperatures varied around 1.3°C ± 1.2°C during early winter, as opposed to 5.0°C ± 1.0°C during late winter.

Analyses of the climate variables showed that the cumulative snowfall was strongly correlated with the corresponding average snow depths (November to January: $n = 20$, $r = 0.69$, $P < 0.001$; February to April: $n = 20$, $r = 0.77$, $P < 0.0001$). We also detected positive relationships between average snow depth during November–January and the subsequent winter period of February–April ($n = 20$, $r = 0.52$, $P < 0.02$), as well as between the cumulative snowfall during November–January and average snow depth during the period of February–April ($n = 20$, $r = 0.57$, $P < 0.01$). These latter 2 relationships reflected the fact that snow that fell during the early winter also contributed to the snowpack in late winter. To avoid effects of autocorrelation in the time series analyses, we subsequently decided to use only the independent measures of cumulative snowfall during the early and late winter periods.

For none of the winter variables was a statistically significant change detected over the course of the study (i.e., between 1989 and 2008; for all, $n = 20$, $P > 0.05$). Precipitation during the summer months of June to August exhibited considerable interannual variation, with a mean cumulative rainfall of 425 ± 105 mm. In all years, however, rainfall exceeded 300 mm. Average daily air temperatures during the corresponding season varied only moderately, with a mean of 17.5°C ± 0.9°C. We detected no significant temporal trend for either of the 2 parameters (for both, $n = 20$, $P > 0.05$).

Population size.—Between 1990 and 2008 the mean number of animals recorded annually varied around 190.9 ± 27.5, with a minimum of 138 in the year 2000 and maximum of 237 animals in the year 2008 (Fig. 2). Over all years together, we estimated an average of 78.3 ± 14.0 adult females, 49.8 ± 12.5 adult males, 20.9 ± 6.6 yearlings, and 41.8 ± 7.3 juveniles. According to the Pearson correlation coefficients, none of these 4 animal categories was significantly correlated with the others in terms of their abundance (for all, $n = 19$, $P > 0.05$).

Model selection.—The best models based on the AIC_c values typically corresponded to the minimal models identified by backward stepwise regression containing only the remaining significant or nearly significant terms. In some cases, competing models (within 2 AICc points) with more variables existed; however, all of the competing models differed only in 1 or 2 additional nonsignificant parameters from the best supported models. Therefore, the main results and interpretations are not directly affected by selection of the most parsimonious models compared with their competing models.

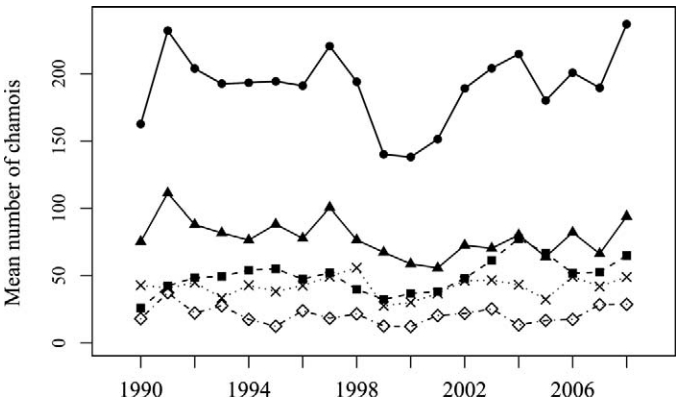

Fig. 2.—The average number of Alpine chamois (*Rupicapra rupicapra*) in the Augstmatthorn National Game Reserve, Switzerland detected per year and within each sex–age class between 1990 and 2008: total of all observed animals (filled circles), adult females (filled triangles), adult males (filled squares), yearlings (open diamonds), and juveniles (x-signs).

Population growth.—Time series regressions revealed that the overall population growth rate, as well as the growth rates within the various sex–age categories, all showed strong effects of negative density dependence at a time lag of 1 year (Table 2). Hence, animal numbers in 1 year negatively influenced the population growth in the subsequent year.

With regard to the climate variables, the Gompertz and Ricker models both showed that cumulative snowfall during the late winter period of the current year (i.e., at time t) was an important determinant negatively affecting the overall population growth (Fig. 3). Slightly nonsignificant terms of snowfall during the late winter period of the previous year (i.e., at time $t - 1$) indicated that snow also might have a lagged effect on population growth. Overall population growth appeared not to be affected by air temperatures or by summer precipitation (Table 2).

Closer examination revealed that the climate effects influenced the various sex–age categories of animals differently. Hence, whereas snow conditions during the late winter of the current year significantly affected the growth rate of the male population, they had no apparent effect on the growth rate of the female population (Table 2). The female segment of the population only responded negatively to cumulative snowfall during the early winter period in the preceding year (i.e., at a time lag of $t - 1$). The cumulative snowfall over the whole winter of the current year and the early winter period of the previous year both negatively influenced the growth of the yearling population. The change in juvenile numbers, however, was negatively affected by the cumulative snowfall during the late winter period of the current year and the early winter of the previous year. Interestingly, numbers of males and yearlings

Table 2.—Selected Gompertz and Ricker models based on the corrected Akaike information criterion (AIC_c) values to estimate the effect of winter snowfall, summer precipitation, and air temperatures during the current (t) and the previous year ($t - 1$) on the change in total population size, and in the 4 different sex–age categories of Alpine chamois (*Rupicapra rupicapra*) in the Augstmatthorn National Game Reserve, Switzerland. The number of animals present in the study area in the year $t - 1$ is n_{t-1}. The abbreviations of the various weather factors are listed in Table 1. Effect sizes ($\bar{X} \pm SE$) of the factors are shown, with significant terms in bold (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$), and terms close to significance in italics.

Model	Total	Adult females	Adult males	Yearlings	Juveniles
Gompertz					
Intercept	**5.52 ± 1.28*** **	**3.72 ± 0.93** **	**2.52 ± 0.50*** **	**7.68 ± 1.12*** **	**3.10 ± 067*** **
Ln(n_{t-1})	**−0.97 ± 0.23*** **	**−0.79 ± 0.21** **	**−0.45 ± 0.12** **	**−1.36 ± 0.14*** **	**−1.11 ± 0.18*** **
SnowF_NDJ$_t$				**−0.34 ± 0.05** **	
SnowF_FMA$_t$	**−0.06 ± 0.02** **		**−0.09 ± 0.02** **	**−0.10 ± 0.02** **	**−0.09 ± 0.02** **
SnowF_NDJ$_{t-1}$		**−0.07 ± 0.03***		**−0.24 ± 0.04*** **	**0.10 ± 0.04***
SnowF_FMA$_{t-1}$	*−0.04 ± 0.02*[a]				
Temp_NDJ$_t$			**−0.23 ± 0.07** **	**−0.62 ± 0.16** **	**0.36 ± 0.09** **
Temp_FMA$_t$				**−0.10 ± 0.03***	**0.08 ± 0.03***
Temp_JJA$_{t-1}$					
Temp_NDJ$_{t-1}$					
Temp_FMA$_{t-1}$				**0.09 ± 0.03***	
Rain_JJA$_{t-1}$					
Ricker					
Intercept	**1.46 ± 0.32*** **	**1.05 ± 0.24*** **	**1.18 ± 0.23*** **	**6.48 ± 1.24*** **	0.17 ± 0.33
n_{t-1}	**−0.005 ± 0.001*** **	**−0.01 ± 0.003** **	**−0.009 ± 0.003** **	**−0.069 ± 0.010*** **	**−0.029 ± 0.004*** **
SnowF_NDJ$_t$				**−0.41 ± 0.09*** **	
SnowF_FMA$_t$	**−0.06 ± 0.02** **		**−0.09 ± 0.02** **	**−0.12 ± 0.04** **	**−0.08 ± 0.02** **
SnowF_NDJ$_{t-1}$		**−0.001 ± 0.0003***		**−0.26 ± 0.06*** **	**0.10 ± 0.04***
SnowF_FMA$_{t-1}$	*−0.04 ± 0.02*[a]				
Temp_NDJ$_t$			**−0.22 ± 0.08***	**−0.87 ± 0.25** **	
Temp_FMA$_t$				**−0.13 ± 0.05***	
Temp_JJA$_{t-1}$					
Temp_NDJ$_{t-1}$					**0.37 ± 0.09** **
Temp_FMA$_{t-1}$					**0.08 ± 0.03***
Rain_JJA$_{t-1}$					

[a] $P = 0.06$.

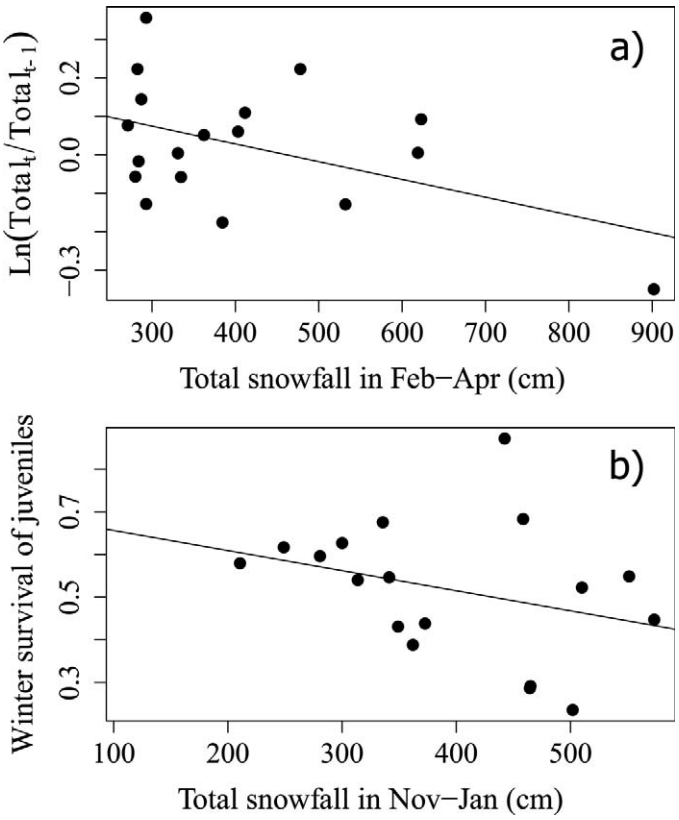

Fig. 3.—Relationships between cumulative snowfall (snow data provided by the Swiss Federal Institute for Snow and Avalanche Research, 2008) and a) the population growth rate, and b) the winter survival of juveniles of Alpine chamois (*Rupicapra rupicapra*) in the Augstmatthorn National Game Reserve, Switzerland.

both responded negatively to increasing current winter air temperatures, whereas positive effects of air temperatures were evident for juveniles during the whole winter of the current year when considering the Gompertz model. Under the Ricker model, this effect was no longer significant, but instead we detected positive effects of winter temperatures at time-lag $t - 1$ for juveniles (Table 2). The cumulative rainfall during the preceding summer did not significantly affect any of the 4 different sex–age categories (Table 2).

Fecundity and survival of juveniles.—The juvenile–female ratio in the study population was significantly negatively affected by the current density of adult females, but interestingly, did not respond to any climate variable (Table 3). Juvenile density in the summer had a negative effect on their subsequent winter survival (Table 3). The cumulative snowfall during the early winter period of the current year and the preceding year both negatively influenced the survival of juveniles (Fig. 3).

Discussion

Density dependence.—Our analyses showed that animal densities during the preceding years always negatively affected the change in animal numbers in the subsequent years. Hence,

Table 3.—Selected models based on the corrected Akaike information criterion (AIC_c) values to estimate the effect of winter snowfall, summer precipitation, and air temperatures during the current (t) and the previous year ($t - 1$) on the juvenile–female ratio and the juvenile winter survival of Alpine chamois (*Rupicapra rupicapra*) in the National Game Reserve "Augstmatthorn" (Switzerland). The abbreviations of the various factors are listed in Table 1. Displayed are the effect sizes of the factors (± *SE*). Significant terms in bold (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Factor	Juvenile–female ratio	Juvenile winter survival
Intercept	0.04 ± 0.26	**1.62 ± 0.57****
nf[a]	**−0.007 ± 0.003***	
nj_{t-1}[b]		**−0.03 ± 0.01****
$SnowF\_NDJ_t$		**−0.13 ± 0.06***
$SnowF\_FMA_t$		
$SnowF\_NDJ_{t-1}$		**−0.19 ± 0.05*****
$SnowF\_FMA_{t-1}$		
$Temp\_NDJ_t$		
$Temp\_FMA_t$		
$Temp\_JJA_{t-1}$		
$Temp\_NDJ_{t-1}$		
$Temp\_FMA_{t-1}$		
$Rain\_JJA_{t-1}$		

[a] nf = number of adult females.
[b] nj = number of juveniles.

evidence exists for direct density dependence in our population of Alpine chamois. These effects also remained significant when the various sex and age categories of animals were considered separately. Accordingly, it can be assumed that resource competition is of major importance for the demography of this Alpine chamois population. This applies particularly to adults, which often segregate sexually outside the mating season (Krämer 1969), but it was also true for subadults and juveniles in our study. Direct density dependence has been reported to occur in a variety of other ungulate populations (for an overview—Wang et al. 2009; Alpine ibex, *Capra ibex*—Grotan et al. 2008; Jacobson et al. 2004; Saether et al. 2007; reindeer, *Rangifer tarandus*—Solberg et al. 2001; red deer, *Cervus elaphus*—Forchhammer et al. 1998; musk ox, *Ovibos moschatus*—Forchhammer et al. 2002). However, 1 study on the population dynamics of Alpine chamois in the Italian Alps failed to find significant effects of direct density dependence on the overall population growth rate (Capurro et al. 1997). Instead, the existence of delayed density dependence was verified. The authors of that study proposed that density effects in their population might be the result of infections with gastrointestinal parasites.

Considering that winter survival of juveniles in our study population depended directly on the observed numbers of juveniles during the preceding summer, resource competition can be assumed to act on this age class as well. However, because juveniles are normally not weaned until late autumn (Ruckstuhl and Ingold 1999), it is likely that competition is mediated by the body condition of mothers. Support for this speculation comes from the 2 following relationships: First, and in accordance with another study on Alpine chamois populations (Pioz et al. 2008a), our analyses showed that the

juvenile–female ratio was negatively affected by the current female density in the population, giving rise to the assumption that heavy intrafemale competition might lead to depressed fecundity rates. Second, the number of juveniles in the population depended strongly on the juvenile numbers in the year before, which is suggesting that successful reproduction in 1 year might negatively affect the likelihood of reproduction during the following year. Hence, it appears as if individual females in our population might be challenged to reproduce successfully in 2 subsequent years. This impression is supported by a study on the reproductive success of females conducted in the study area (Baumann 1993). Accordingly, it was shown that individual females that raised a kid in 1 year were less likely to give birth in the following year. Similar relationships were reported for female red deer (Clutton-Brock et al. 1982) and other ungulates (e.g., Coulson et al. 2000; Kruuk et al. 1999).

Climate effects.—While accounting for effects of density dependence, our study furthermore showed, in agreement with studies on other mountain ungulates (e.g., Grotan et al. 2008), that the cumulative amount of snowfall during the late winter period of the current year had a negative effect on the change in total population size. Thus, as expected, heavy snowfall toward the end of the winter seemed to substantially limit population growth in Alpine chamois. This interpretation is supported by the population response following the winter of 1999, which was characterized by exceptionally strong snowfalls. Accordingly, strong declines in animal numbers often are triggered by extreme and unusual events (Stenseth et al. 2002). Similar findings have been reported for other species, such as Alpine ibex (Jacobson et al. 2004) and mountain goats (White et al. 2011), 2 other ungulates inhabiting extreme alpine environments throughout the year.

Considering that body condition of Alpine chamois deteriorates steadily during winter (Schröder 1971), the finding that the amount of snowfall during late winter might limit population growth is not a surprise. A recent study on the spatiotemporal patterns of mortality of Alpine chamois in another part of Switzerland supports this assumption; chamois fatalities in that area typically peaked during the late winter period (i.e., between February and April—Jonas et al. 2008). In that study, average snow depth during the whole winter was revealed to be the crucial factor contributing positively to chamois mortality in that area (Jonas et al. 2008). Comparable results were detected in mountain goats inhabiting the coastal range of Alaska, and there, animal mortality also increased toward the end of the winter (White et al. 2011).

Population growth in our study also appeared to be affected slightly by the amount of snow in the previous winter (i.e., at time $t - 1$). This result suggests that severe winter conditions with a lot of snow might not only act in the short term, but also might cause long-lasting effects that are still detectable in subsequent years. Assuming that this is indeed the case, this finding implies that animals might not always be able to recover completely from severe winters during the following summer, carrying over conditional deficits to the next winter. Comparable results pointing in the same direction also were obtained for some populations of Alpine ibex in Switzerland (Grotan et al. 2008). Additional support also is provided by a study on the effects of climate on life history traits in moose (*Alces alces*) by Veeroja et al. (2008). Those authors demonstrated that severe winter conditions during previous years significantly limited jawbone growth, and hence, growth in body size of adult females in subsequent years, giving rise to the assumption that energy reserves might indeed not be replenished within 1 summer.

With regard to sex–age classes, strong impacts of late winter snow on the change in animal numbers were revealed for adult males, yearlings, and juveniles, but not for adult females. Thus, as predicted, the number of females appeared to be largely unaffected by snow conditions during the winter, which is congruent with the observation that adult females typically lose less weight than adult males during the winter months (Schröder 1971). But the fact that growth of the juvenile segment of the population, as well as winter mortality of juveniles, all responded to the cumulative snowfall recorded during the preceding winter (hence, when the juveniles were still unborn) suggests that adult females were negatively affected by harsh winters with a lot of snow. Instead of showing a numerical response, they displayed a differential reproductive success, which was reflected by the change in the number of juveniles born and raised during the subsequent summer, and the proportion of juveniles that survived to yearling age. Again, these results support the assumption that female body condition at the end of the winter is an important determinant of the subsequent reproductive success in female ungulates (Clutton-Brock et al. 1982; Coulson et al. 2000; Kruuk et al. 1999; but see Pioz et al. 2008b).

The finding that growth rates of the yearling and male segments of the population were both strongly influenced by late winter conditions also suggested that juveniles and males seem to be more susceptible to adverse environmental conditions than females (Toigo and Gaillard 2003). One likely reason for this is that both males and juveniles typically possess lower energy reserves when entering the winter. The reduced fat reserves of males are to a major extent the direct consequence of increased levels of energy expenditures during the rut, together with a heavily depressed food intake at the same time (Willisch and Ingold 2007). Thus, males can lose up to 40% of their body weight during the rut (Schröder 1971). Therefore, if winter conditions become increasingly difficult, males might no longer have sufficient fat reserves to cope with limited food resources and elevated energy expenditures, making them particularly vulnerable to death due to starvation and exhaustion.

Regarding the response of the yearling numbers to varying snow conditions, another part of the explanation might lay in the physiological constraints faced by small-sized animals in general. Small animals not only have higher metabolic needs per unit of body weight than their bigger conspecifics (Hudson and White 1985; Van Soest 1994), but they are also less efficient in extracting energy from poor-quality food (Illius and

Gordon 1992). As a consequence, juveniles are, in fact, obliged to acquire more energy relative to their body weight than older animals to meet basic metabolic needs. Furthermore, as small-sized animals, juveniles are likely to incur higher energetic costs of locomotion than adults when roaming in snow-covered areas, which would additionally strain their energy budget. Therefore, it is not surprising that survival of juveniles in winter strongly responded to the current snow conditions. Hence, winters with a lot of snow are likely to limit considerably the recruitment of juveniles into the adult population, a pattern also observed in isards (*Rupicapra pyrenaica*), a close relative of the Alpine chamois (Crampe et al. 2002; Gonzalez and Crampe 2001).

Considering the effects of air temperatures, the animal categories that responded most to the corresponding variables were juveniles and yearlings, followed by adult males. Accordingly, the change in the juvenile population was positively related to temperatures during the current winter for the Gompertz model and during the previous winter for the Ricker model, indicating that thermoregulatory effects might have a marked influence on the body condition of females and their ability to conceive and successfully reproduce later on. Similar results were reported for Saiga antelope (*Saiga tatarica*), Soay sheep (*Ovis aries*), red deer (Coulson et al. 2000), and elk (*Cervus canadensis*—Wang et al. 2002). Furthermore, benefits of warm winter temperatures might be mediated by negative effects on the bacterial populations prevalent in the study area, which are known to cause reproductive failures in Alpine chamois, as recently evidenced by Pioz et al. (2008a).

Equivocal and somewhat counterintuitive results were obtained for adult males and yearlings. Thus, temperatures during the current winters were negatively correlated with subsequent changes in the male and yearling segments of the population. This could mean that winter temperatures as a thermoregulatory factor might only be of minor importance; otherwise we should have detected the opposite pattern. Possibly, the lower air temperatures had a positive effect on the load-carrying capacity of the upper snow layer, enabling animals to cross snow-covered areas with less energetic effort (Parker et al. 1984). This might be particularly important for animals with low energy reserves, such as young animals and adult males during and after the rut.

In contrast to other ungulates (e.g., Grotan et al. 2008), no significant effects of summer precipitation on the population growth rates of our Alpine chamois could be detected. This is interesting since Loison et al. (1999) proposed that climate effects in populations of isards and Alpine chamois might also operate indirectly through the development of the vegetation. It is possible that summer rainfall in our study area had no marked, limiting effect on vegetation growth and quality, and consequently on the chamois population. This supposition is reasonable given the fact that summer precipitation never dropped below 300 mm. Furthermore, suitable summer habitat of Alpine chamois extends over a much larger area than the heavily confined winter habitat, providing virtually unlimited, high-quality forage during the time of vegetation growth.

Population dynamics and climate change.—Although negative density dependence and, therefore, direct resource competition seem to play an important role in the dynamics of Alpine chamois and other ungulates, our study indicated that the prevailing snow conditions during winter appear to be the driving extrinsic force of change in the population we studied. With regard to the important phenomenon of global warming, plausible forecasts about how Alpine chamois populations will respond to changing environments are difficult to construct. The fact that yearlings and males, in contrast to juveniles, responded negatively to increasing winter temperatures makes it challenging to predict the direction of expected changes in the dynamics of the populations. Overall, it is reasonable to assume, however, that fluctuations in Alpine chamois populations might become larger if winter conditions become more variable in the future.

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Literature Cited

Baumann, M. 1993. Dominance, resource competition and differential reproductive success within a female home-range group of Alpine chamois (*Rupicapra rup. rupicapra* L.). Diploma thesis, University of Bern, Bern, Switzerland.

Baur, J. J. 1985. Fecundity patterns of stable and colonising chamois populations of New Zealand and Europe. Pp. 154–165 in The biology and management of mountain ungulates (S. Lovari, ed.). Croom Helm, London, United Kingdom.

Bobek, B., K. Perzanowski, and J. Weiner. 1990. Energy expenditure for reproduction in male red deer. Journal of Mammalogy 71:230–232.

Boldt, A. 2003. Habitat use and activity of female Alpine chamois (*Rupicapra rupicapra*) in winter affected by air traffic, snow and weather. University of Bern, Bern, Switzerland.

Capurro, A. F., M. Gatto, and G. Tosi. 1997. Delayed and inverse density dependence in a chamois population of the Italian Alps. Ecography 20:37–47.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer. Behavior and ecology of two sexes. The University of Chicago Press, Chicago, Illinois.

Coulson, T., E. J. Milner-Gulland, and T. H. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proceedings of the Royal Society of London Series B–Biological Sciences 267:1771–1779.

Coulson, T., et al. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Crampe, J. P., J. M. Gaillard, and A. Loison. 2002. Winter snowfall: a variable factor in recruitment by isard populations (*Rupicapra pyrenaics pyrenaica*). Canadian Journal of Zoology 80:1306–1312.

Crawley, M. J. 2007. The R book. John Wiley & Sons Ltd., Chichester, United Kingdom.

Forchhammer, M. C., E. Post, N. C. Stenseth, and D. M. Boertmann. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. Population Ecology 44:113–120.

Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society of London Series B–Biological Sciences 265:341–350.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gander, H., and P. Ingold. 1997. Reactions of male Alpine chamois *Rupicapra r rupicappa* to hikers, joggers and mountain bikers. Biological Conservation 79:107–109.

Garel, M., A. Loison, J. M. Jullien, D. Durbay, D. Maillard, and J. M. Gaillard. 2009. Sex-specific growth in Alpine chamois. Journal of Mammalogy 90:954–960.

Gonzalez, G., and J. P. Crampe. 2001. Mortality patterns in a protected population of isards (*Rupicapra pyrenaica*). Canadian Journal of Zoology 79:2072–2079.

Grotan, V., B. E. Saether, F. Filli, and S. Engen. 2008. Effects of climate on population fluctuations of ibex. Global Change Biology 14:218–228.

Grothendieck, G. 2009. dyn: time series regression. http://cran.r-project.org/web/packages/dyn/dyn.pdf. Accessed 7 September 2009.

Hamr, J. 1985. Seasonal home range size and utilisation by female chamois (*Rupicapra rupicapra* L.) in northern Tyrol. Pp. 106–116 in The biology and management of mountain ungulates (S. Lovari, ed.). Croom Helm, London, United Kingdom.

Hudson, R. J., and R. G. White. 1985. Bioenergetics of wild herbivores. CRC Press, Inc., Boca Raton, Florida.

Hurvich, C. M., and C. L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Illius, A. W., and I. J. Gordon. 1992. Modeling the nutritional ecology of ungulate herbivores—evolution of body size and competitive interactions. Oecologia 89:428–434.

Ingold, P., U. Pfister, E. Baechler, and P. Enggist-Dueblin. 1998. Pattern and rhythm of activity in alpine chamois (*Rupicapra r. rupicapra*) during winter. Zeitschrift für Säugetierkunde 63:183–185.

Jacobson, A. R., A. Provenzale, A. von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598–1610.

Jenouvrier, S., H. Caswell, C. Barbraud, M. Holland, J. Stroeve, and H. Weimerskirch. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. Proceedings of the National Academy of Sciences 106:1844–1847.

Jonas, T., F. Geiger, and H. Jenny. 2008. Mortality pattern of the Alpine chamois: the influence of snow-meteorological factors. Annals of Glaciology, 49:56–62.

Krämer, A. 1969. Soziale Organisation und Sozialverhalten einer Gemspopulation (*Rupicapra rupicapra* L.) der Alpen. Zeitschrift für Tierpsychologie 26:889–964.

Kruuk, L. E. B., T. H. Clutton-Brock, S. D. Albon, J. M. Pemberton, and F. E. Guinness. 1999. Population density affects sex ratio variation in red deer. Nature 399:459–461.

Lele, S., M. L. Taper, and S. Gage. 1998. Statistical analysis of population dynamics in space and time using estimating functions. Ecology 79:1489–1502.

Loison, A., G. Darmon, S. Cassar, J. M. Jullien, and D. Maillard. 2008. Age- and sex-specific settlement patterns of chamois (*Rupicapra rupicapra*) offspring. Canadian Journal of Zoology 86:588–593.

Loison, A., J. M. Jullien, and P. Menaut. 1999. Relationship between chamois and isard survival and variation in global and local climate regimes: contrasting examples from the Alps and Pyrenees. Ecological Bulletins 47:126–136.

McElligott, A. G., F. Naulty, W. V. Clarke, and T. J. Hayden. 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? Evolutionary Ecology Research 5:1239–1250.

Mysterud, A., C. Bonenfant, L. E. Loe, R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2008. Age-specific feeding cessation in male red deer during rut. Journal of Zoology (London) 275:407–412.

Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. Journal of Zoology (London) 264:209–215.

Mysterud, A., and E. Ostbye. 2006. Effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes: the Lier Valley, Norway. Wildlife Biology 12:321–329.

Ozgul, A., et al. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637–669.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Cote. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pioz, M., et al. 2008a. Diseases and reproductive success in a wild mammal: example in the alpine chamois. Oecologia 155:691–704.

Pioz, M., A. Loison, P. Gibert, J. M. Jullien, M. Artois, and E. Gilot-Fromont. 2008b. Antibodies against salmonella is associated with reduced reproductive success in female alpine chamois (*Rupicapra rupicapra*). Canadian Journal of Zoology 86:1111–1120.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/. Accessed 10 November 2011.

Ruckstuhl, K. E., and P. Ingold. 1999. Aspects of mother–kid behavior in Alpine chamois, *Rupicapra rupicapra rupicapra*. Zeitschrift für Säugetierkunde 64:76–84.

Saether, B. E., M. Lillegard, V. Grotan, F. Filli, and S. Engen. 2007. Predicting fluctuations of reintroduced ibex populations: the importance of density dependence, environmental stochasticity and

uncertain population estimates. Journal of Animal Ecology 76:326–336.

SCHNIDRIG-PETRIG, R., AND P. INGOLD. 2001. Effects of paragliding on alpine chamois *Rupicapra rupicapra rupicapra*. Wildlife Biology 7:285–294.

SCHRÖDER, W. 1971. Untersuchungen zur Ökologie des Gamswildes (*Rupicapra rupicapra* L.) in einem Vorkommen der Alpen. 1. Teil. Zeitschrift für Jagdwissenschaft 17:113–168.

SCHRÖDER, W., AND I. VON ELSNER-SCHACK. 1985. Correct age determination in chamois. Pp. 65–70 in The biology and management of mountain ungulates (S. Lovari, ed.). Croom Helm, London, United Kingdom.

SIKES, R. S., GANNON, W. L. and THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SOLBERG, E. J., ET AL. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. Ecography 24:441–451.

SOLBERG, E. J., B. E. SAETHER, O. STRAND, AND A. LOISON. 1999. Dynamics of a harvested moose population in a variable environment. Journal of Animal Ecology 68:186–204.

STENSETH, N. C., A. MYSTERUD, G. OTTERSEN, J. W. HURRELL, K. S. CHAN, AND M. LIMA. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

TOIGO, C., AND J. M. GAILLARD. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos 101:376–384.

VAN SOEST, P. J. 1994. Nutritional ecology of the ruminant. 2nd ed. Cornell University Press, Ithaca, New York.

VEEROJA, R., V. TILGAR, A. KIRK, AND J. TONISSON. 2008. Climatic effects on life-history traits of moose in Estonia. Oecologia 154:703–713.

VISSER, M. E. 2010. Fatter marmots on the rise. Nature 466:445–447.

WALTHER, G. R., ET AL. 2002. Ecological responses to recent climate change. Nature 416:389–395.

WANG, G. M., ET AL. 2009. Density dependence in northern ungulates: interactions with predation and resources. Population Ecology 51:123–132.

WANG, G. M., N. T. HOBBS, F. J. SINGER, D. S. OJIMA, AND B. C. LUBOW. 2002. Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado. Climatic Change 54:205–223.

WHITE, K. S., ET AL. 2011. Mountain goat survival in coastal Alaska: effects of age, sex, and climate. Journal of Wildlife Management 75:1731–1744.

WILLISCH, C. S., AND P. INGOLD. 2007. Feeding or resting? The strategy of rutting male Alpine chamois. Ethology 113:97–104.

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